ON THE OVIPOSITION BEHAVIOR OF *MELIPONA COMPRESSIPES FASCICULATA* (HYMENOPTERA, MELIPONINAE)

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ABSTRACT

The provisioning and oviposition process (POP) in the stingless bees *Melipona compressipes fasciculata* Smith, 1854, was analyzed and discussed. The following ethological features were observed: (1) the species presents successive cell construction and exclusively batched oviposition cycles (C_cB_e), a singular pattern among all species of *Melipona*; (2) ritualized dominance aspects as to queen/workers interactions; (3) effective trophallaxis between queen and workers.

KEYWORDS. Hymenoptera, Apidae, *Melipona*, oviposition, queen/worker interactions.

INTRODUCTION

The first descriptions related to the systematization of the complex patterns of the oviposition process behavior in Meliponinae were carried out by SAKAGAMI & ZUCCHI (1963) and SAKAGAMI & ZUCCHI (1974).

There are few published papers approaching the provisioning and oviposition process (POP) in *Melipona* Illiger, 1806: *M. compressipes manaosensis* Schwarz, 1932, (SAKAGAMI & ONIKI, 1963), *M. pseudocentris pseudocentris* Cockerell, 1912, (BUSCHINELLI & STORT, 1965), *M. quadrifasciata anthidioides* Lepeletier, 1836, (SAKAGAMI et al., 1965), *M. rufiventris rufiventris* Lepeletier, 1836, (CAMILLO, 1972).

The Meliponinae phylogeny has been done mainly based on morphological characters (MOURE, 1951,1961; MICHENER & GRIMALDI, 1988; PRENTICE, 1991; CAMARGO & PEDRO, 1992; CAMARGO & MOURE, 1996). However, well established intranidal behavior features can present the same value when compared to the morphological ones (MICHENER, 1953; SAKAGAMI & YOSHIKAWA, 1968).

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This paper reports the provisioning and oviposition process (POP) and types of queen/workers interactions in *M. compressipes fasciculata* Smith, 1854. The main behavior observed was characterized ethologically and compared with other *Melipona* species.

MATERIAL AND METHODS

The colonies of *M. c. fasciculata* were collected in Arari, Maranhão State in October, 1989, and observed in heated observation hives in Ribeirão Preto, São Paulo, Brazil. The provisioning and oviposition process (POP) was studied from February to December, 1990.

Colony conditions were evaluated twice, at the beginning and at the end of the observations in order to verify the state of the colony. The number of honey and pollen pots and the number of combs in several stages of development were used as parameters (tab.I).

Table I. General colony conditions in *Melipona compressipes fasciculata.*

Colony conditions	Mar, 20 1990	Dec, 03 1990
Number of pollen pots	open 3	open 5
	closed 2	closed 29
Number of honey pots	open 3	open 7
	closed 2	closed 28
Number of fresh combs	6	3
Number of older combs	3	6

The methodology used for the observations related to the frequency of queen/workers interactions was applied during the first 5 minutes of the beginning, middle and end of ($\overline{Q}+\overline{T}+\overline{P}$), and during $\overline{A}$ and $\overline{pr}$. Also, the first 5 minutes of the end of ($\overline{Q}+\overline{T}+\overline{P}$) and the totality of $\overline{A}$ were considered for the analysis of food begging and trophallaxis behavior.

The observation procedure and some terminology was based on Sakagami & Zucchi (1974) **apud** DRUMOND **et al.** (1977). The POP of stingless bees is composed of: 1) Periods: Quiescent ($\overline{Q}$), comb surface without agitation. From the end of the prior $\overline{O}$ to the revival of some agitation, such as the first visit by the queen to the brood cell area. Transient ($\overline{T}$), from the end of $\overline{Q}$ to the start of $\overline{O}$. 2) Stages: Patrolling ($\overline{P}$), from the queen's first visit to the brood cell area to the start of $\overline{A}$. Arousal ($\overline{A}$), from the queen's final visit to the brood cell area to the start of $\overline{O}$'. Oviposition ($\overline{O}$'), from the queen's final arrival at a collared (= structurally finished) cell to the completion of the operculation of the last oviposited cell. 3) Phases: Preprovisioning ($\overline{p}$), from the start of the queen's final waiting by the cell to the first food discharge in the cell by a worker. Provisioning ($\overline{pr}$), from the first to the last food discharge in the cell. Postprovisioning ($\overline{ps}$), from the last food provisioning to the start of $\overline{o}$. Oviposition ($\overline{o}$). from the pre-oviposition cell inspection by the queen to the end of the queen's oviposition. Sealing ($\overline{s}$), with four subphases, Preoperculation ($\overline{s_p}$), rotation ($\overline{s_r}$), transient ($\overline{s_t}$) and sidework ($\overline{s_s}$).

RESULTS AND DISCUSSION

Cell construction. The construction of each brood cell is characterized as successive type (C_c), i.e., at any time there are cells in several phases of development. The number of cells in construction was 23.8 ± 5.4 (11< value > 37 cells, n = 40) (tab. II). The species built concentric and horizontal combs characterized by irregular expansion. The temporal succession in cell construction (fig.1, tab. III) and the necessary time for cell accomplishment was of approximately 10 hours.

Table II. Presence of brood cells in different development stages in *Melipona compressipes fasciculata*. (INN, cells at the very beginning; IN, shell-shaped cells; 1/4 - 1/2 - 3/4 - 4/4 , related to the size of operculated cells; CO, higher collared cell in relation to the operculated one). x = 23.8 ± 5.4 cells (n = 40).

Observations	INN	IN	1/4	1/2	3/4	4/4	CO	Total
01	1	1	1	-	2	3	7	15
02	3	1	1	1	-	2	3	11
03	3	1	2	1	3	9	7	26
04	4	2	1	-	2	3	5	17
05	4	3	1	1	1	5	7	22
06	3	1	1	3	4	1	3	16
07	-	1	1	5	3	6	9	25
08	2	1	1	1	2	4	4	15
09	4	3	-	4	6	4	3	24
10	2	2	3	1	4	3	8	23
11	3	3	3	3	4	4	10	30
12	2	4	-	4	3	5	2	20
13	1	3	3	1	6	5	5	24
14	5	1	1	-	6	2	7	22
15	2	5	3	4	5	3	11	33
16	3	2	2	4	6	5	9	31
17	2	-	1	6	8	5	7	29
18	3	4	-	1	4	4	6	22
19	4	1	2	4	3	5	4	23
20	4	1	-	3	3	2	8	21
21	4	5	1	1	3	6	10	30
22	4	5	1	3	6	2	2	23
23	1	5	1	1	8	4	4	24
24	1	2	1	2	3	6	7	22
25	3	4	3	4	2	5	8	29
26	2	1	2	2	3	3	5	18
27	3	-	2	3	2	6	6	22
28	4	3	2	1	1	3	5	19
29	4	2	4	3	4	3	6	26
30	5	4	3	2	1	3	7	25
31	2	2	1	3	6	4	6	24
32	3	2	6	2	4	1	6	24
33	2	3	1	1	4	7	3	21
34	4	2	1	3	6	1	4	21
35	1	2	5	5	3	4	9	29
36	2	2	2	2	3	6	6	23
37	6	1	2	3	4	2	10	28
38	2	3	4	3	3	1	6	22
39	4	2	3	10	10	1	4	34
40	3	5	2	6	5	2	14	37

According to Camillo-Atique (1974) and Sakagami & Zucchi (1974), the number of cells built in the colony depends on the general colony conditions as well as on the amount of food, size of population, among other factors.

Type of oviposition process. Batched and singular ovipositions were found, 87.8% of them formed batches (n= 49). The percentage of singular ovipositions occurred

Table III. Duration of brood cells construction (min) in *Melipona compressipes fasciculata*. * See table II; PO, queen oviposition.

Stages	Average time (x) (min.)	Number of processes
INN- 1/4*	164.0 ± 83.2	15
1/4 - 1/2	55.0 ± 27.5	24
1/2 - 3/4	85.2 ± 51.7	25
3/4 - 4/4	169.6 ± 97.5	26
4/4 - CO	120.9 ± 72.9	32
CO - PO	200.0 ± 125.3	21
INN - CO	Σx=594.7 ou 10 h	
INN - PO	Σx=794.7 ou 13 h	

during the winter, when the colony was weaker due to external low temperature and to the small availability of vegetal species for the bees as compared to periods with more resources along the year. The cell construction pattern for *M. c. fasciculata* was considered exclusively batched (B_e).

These features were found only in this species. Thus, *M. c. fasciculata* is considered C_cB_e type, while other *Melipona* species belong to types C_sB_s or C_cB_f. The number of oviposited cells per oviposition process was 5.6 ± 2.5 (1< value >11 cells, n = 48); the interval between two ovipositions in the same process was 22.9 ± 18.7 (5 < value > 103 sec., n = 28), and the interval between two consecutive processes was 301.3 ± 74.8 min (3 < value > 7h and 50 min, n = 24). At the end of the oviposition process, non-oviposited collared cells were always verified. The number of these cells was 2.9 ± 1.5, (1 < value > 6 cells, n = 34). Colonial productivity in 24 h was around 27 ovipositions per day.

Taking into account the time during which the queen appeared out of comb after the last oviposition and adding it to the time when she stayed on the comb, excluding stages $\overline{A}$ and $\overline{O}$', it was possible to determine $(\overline{Q}+\overline{T}+\overline{P})$, 237.7 ± 59.0 (160.5 < value > 389.8 min, n = 20), which corresponded to 4h.

Queen/workers interactions. When the queen met a worker, she touched her vertex with her antennae, forelegs and mandibles. The reaction of the worker was vertex presentation or, in some cases, escape by quickly changing direction. Another type of interaction presented was the advance-retreat behavior, i.e., the worker dashed toward the queen, and retreated. This type of behavior was repeated several times. Sometimes the darting attitude was displayed and the worker strongly hit the queen's face (fig. 2); in other circumstances the queen walked on the new brood cells and touched workers that were building cells at any stage of development with her antennae and forelegs. These interactive behaviors occurred in $(\overline{Q}+\overline{T}+\overline{P})$ and $\overline{A}$ (tab. IV).

In almost all species of *Melipona* up to now studied, there is remarkable ritualization between the queen and workers as it is observed in *M. c. fasciculata* with some variations. The advance-retreat behavior when the two castes are close is very common. Another constant behavior is the presentation of body parts by workers representing a submissive behavior as in *M. q. anthidioides*, *M. s. merrilae* Cockerell, 1919, and *M. r. rufiventris*, (BEIG & SAKAGAMI, 1964; SAKAGAMI **et al.**, 1965; CAMILLO-ATIQUE, 1974).

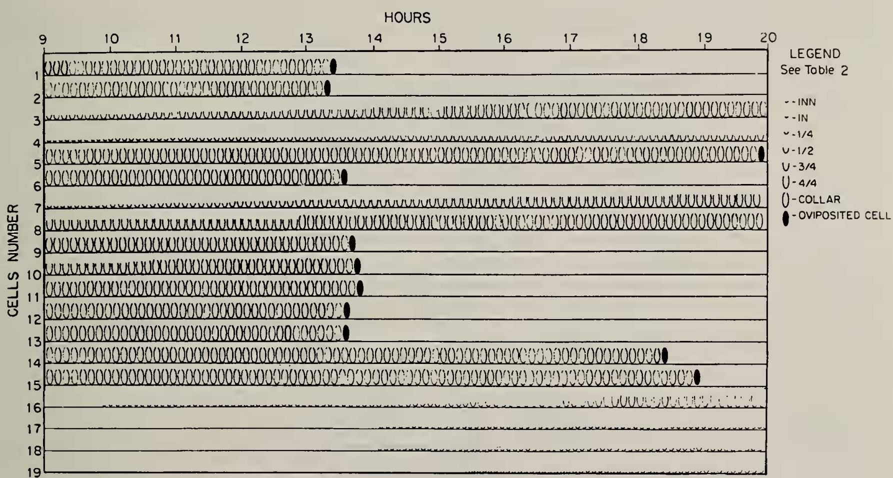

Fig. 1. Cell construction and oviposition sequences of POP recorded in the colony of *Melipona compressipes fasciculata* during 11h of observation. See Table II.

When the queen of *M. c. fasciculata* was resting on the brood comb, she trembled her body, rhythmically beat her wings and formed a small royal court (3 to 6 workers) (fig. 2). Such court did not follow the queen when she was walking. Sometimes the court was composed of up to 10 bees. The attending bees participating in the royal court bent their bodies, with or without wing beating; they touched the body of the queen performing advance-retreat movements with their antennae (tab. IV).

Sakagami & Oniki (1963), working with *M. c. manaosensis,* demonstrated that if the queen continues to rest at the same place, a weak royal court is gradually formed, the number of attendants never exceeding six, but this may mostly be conditioned by the small colony size. Each attendant stretches her antennae toward the queen, trembling her body with repetition of rapid advances-retreats. These rhythmic movements are especially conspicuous in the workers standing in front of the queen. Such workers occasionally make short but violent dashing movements towards the queen as if attacking her. In such royal court, the touching of the queen with their antennae was always observed.

In *M. s. merrillae*, Beig & Sakagami (1964), the formation of the royal court in

Table IV. Frequency of queen/workers interactions in different phases of the POP in *Melipona compressipes fasciculata*. $(\overline{Q}+\overline{T}+\overline{P})$ = out-of-POP period; $\overline{A}$ = arousal stage; $\overline{pr}$= preprovisioning; 1= vertex presentation; 2 = escape; 3 = court; 4 = expulsion by the queen with her antennae and forelegs at the collared cell; 5 = expulsion by the queen with her antennae at the collared cell; 6= advance-retreat; 7 = interruption of cell construction by the queen. The numbers in parenthesis represent the percentage of each behavior.

Interactions	(Q+T+P) beginning	(Q+T+P) middle	Q+T+P) final	A	pr
1	3 (0.5)	5 (1.0)	5 (1.1)	31 (2.6)	-
2	80 (13.2)	47 (9.1)	32 (6.9)	41 (3.4)	-
3	138 (22.8)	114 (22.1)	100 (21.7)	-	-
4	-	9 (1.8)	35 (7.6)	34 (2.9)	153 (82.7)
5	-	-	-	-	32 (17.3)
6	235 (38.8)	164 (31.8)	167 (36.2)	1088 (91.1)	-
7	150 (24.8)	176 (34.2)	122 (26.5)	-	-
Number of interactions (total)	606	515	461	1194	185
Number of observations (total)	40	42	47	45	22

places other than the developing brood comb was virtually absent. This might be partly due to the small colony size, but it is also partly caused by the queen's dashing reaction towards the approaching workers. Because of this reaction, which was seldom observed in *M. c. manaosensis*, the number of royal attendants only rarely exceeded four, even on the comb surface.

SAKAGAMI **et al.** (1965), studying *M. q. anthidioides,* verified the gradual formation of a royal court when the queen stayed quiet for a while. In *M. r. rufiventris,* if the queen rested for a longer period of time, a small court could occur, but it was later interrupted. The number of attendants varied from 1 to 4 (CAMILLO-ATIQUE, 1974).

In *M. c. fasciculata* the advance-retreat behavior performed by workers in their encounters with the queen was the most frequent behavior; whereas, the least frequent behavior was the worker's presenting her vertex to the queen. Two interactions observed with high frequency in $\overline{pr}$ were: worker expulsion by the queen with her antennae and forelegs at the collared cells. The same behavior was shown by the worker using only her antennae, which occurred only in $\overline{pr}$. The worker expulsion by the queen with her antennae and forelegs at the ready cell was begun in the middle of the out-of-POP period and reached maximum peak in $\overline{pr}$ with a lot of aggressiveness. This last behavior in $\overline{pr}$ may be important to promote the beginning of queen oviposition (tab. IV).

According to ZUCCHI (1993), in the *Melipona* genus, queen/worker interactions are characterized: 1) during $\overline{P}$ and $\overline{A}$, the workers presenting akinetic and submissive posture, with presentation of body parts followed by touches with their antennae and forelegs; 2) during $\overline{pr}$, the tapping behavior on the workers who were performing body insertions at a ready cell. The author also mentioned that such ritualized dominance signals are clearly concentrated in $\overline{P}$, $\overline{A}$ and $\overline{pr}$. In the case of *M. c. fasciculata*, such

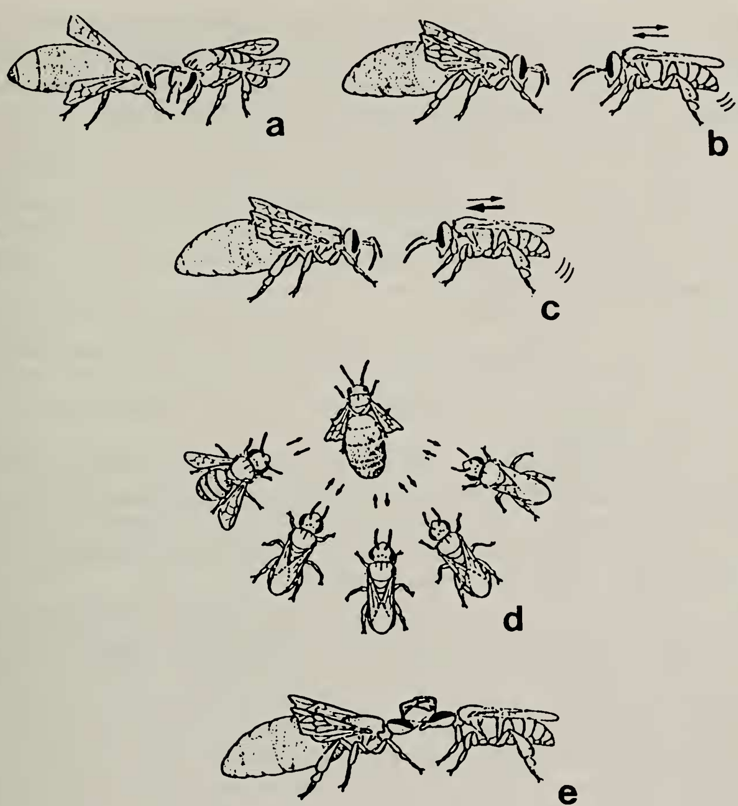

Fig. 2. Some types of queen/workers interactions in *Melipona compressipes fasciculata*: a, vertex presentation; b, advance-retreat; c, darting; d, royal court; e, trophallaxis.

signals are more frequently found in $\overline{P}$ and $\overline{A}$, and never in $\overline{pr}$ (tab. IV).

In *M. c. fasciculata*, the trophallaxis behavior occurred with some ritualizations. The queen presented wing shaking and secured the worker's forelegs with her forelegs. Exchanges of antennae touches also occurred. The queen introduced her tongue between the worker's mandibles which were then open. This fact suggests the food exchange from the worker to the queen. The worker extended her head to the front lower position, suggesting a submissive posture (fig. 2).

As to food begging by the queen, the same behavior cited above was verified, but in this case, without the extending of the worker's head. Instead, she immediately escaped. The number of food begging and trophallaxis by the queen at the end of $(\overline{Q}+\overline{T}+\overline{P})$ were 17.6 ± 12.1 (n=50) and 5.4 ± 9.1 (n=50), respectively. The results obtained for the same behaviors in $\overline{A}$ were 26.0 ± 17.7 (n=20) and 10.1 ± 8.9 (n=20), respectively.

In *M. c. manaosensis,* the queen often eagerly begged food to workers, and buccal contact between them was occasionally observed (SAKAGAMI & ONIKI, 1963). In *M. r. rufiventris,* the queen introduced her tongue between the worker's open mandibles. Then, trophallaxis from worker to queen occurred (CAMILLO-ATIQUE, 1974).

According to SOMMEIJER (1985), in *M. favosa* Fabricius, 1798, the colony queen rarely received food from workers, and this type of behavior evolved into a secondary function, i.e., ritualized behavior expressed the dominance of the queen over the workers. KORST & VELTHUIS (1982), studying *Apis mellifera* Linnaeus, 1758, showed that fewer than 5% of trophallactic interactions resulted in real food transfer, suggesting the ritualized communicative character of such contacts.

In Meliponinae, most queens perform wing movements when they are walking or resting. These types of wing movements present variations as follows: simple strokes intercalated with shaking in *M. r. rufiventris,* (CAMILLO-ATIQUE 1974), discontinuous strokes with low-frequency shaking often mixed with simple strokes in *M. s. merrillae*, (BEIG & SAKAGAMI, 1964).

In *M. c. fasciculata* and *M. c. manaosensis,* each beat is a simple stroke without vibration, (SAKAGAMI & ONIKI, 1963). In *M. c. fasciculata,* the number of wing strokes measured at 30 sec. intervals was 36.5 ± 5.8 (24 < value > 48 strokes, n = 58). These results were recorded when the queen was walking; however, in resting, the number was 47.7 ± 8.7 (20 < value > 60 strokes, n = 60).

One aspect observed in *M. c. fasciculata* was the increase in the number of workers on the new comb in the course of POP (tab. V). These results agree with SAKAGAMI & ZUCCHI (1974), i.e., there is a congestion of workers on the new comb when the queen's oviposition is approaching.

Arousal stage ($\overline{A}$). The characteristic agitation which occurred in $\overline{A}$ increased at particular cells. Therefore, this is a pattern for this species (C<W) as well as a localized type ($A_g<A_l$). This behavior occurs in *M. c. manaosensis* (SAKAGAMI & ONIKI, 1963), *M. q. anthidioides* (SAKAGAMI **et al.**, 1965) and *M. r. rufiventris* (CAMILLO-ATIQUE, 1974).

In this stage, the *M. c. fasciculata* behavior was expressed as cW where the queen was temporarily fixed at the collared cell; in this cell, she always stayed in geonegative position with irregular wing shaking, a trembling abdomen and antennal agitation. Then, she approached and touched the worker with her antennae and forelegs, trying to withdraw the worker (tab. IV). Occasionally, the queen used her median legs and the worker, who was already out of the brood cell, placed the queen on her thorax, supported by her median legs. When the worker did not leave the cell, the queen aban-

Table V. Number of workers on the new brood comb in *Melipona compressipes fasciculata.* ($\overline{Q}+\overline{T}+\overline{P}$) = out-of-POP period; $\overline{A}$ = arousal stage.

Period	n	x and SD	number of workers
$(\overline{Q}+\overline{T}+\overline{P})_{beginning}$	73	17.7 ± 7.8	6 - 36
$(\overline{Q}+\overline{T}+\overline{P})_{middle}$	17	21.2 ± 7.1	12 - 34
$(\overline{Q}+\overline{T}+\overline{P})_{final}$	73	23.6 ± 6.6	10 - 38
$\overline{A}$	73	34.1 ± 10.7	17 - 59

doned such place. This behavior was repeated several times. An interesting aspect was that the cells in which the queen fixed for a longer time were those in the collar stage of the previous oviposition process.

The duration of $\overline{A}$ was 1791.5 ± 1547.6 (36 < value > 4719 sec., n = 20) of about 30 min and the number of cells visited by the queen in $\overline{A}$ was 7.3 ± 6.4 (1 < value> 26 cells, n = 20).

Preprovisioning phase ($\overline{pr}$). In this phase, there was worker agglomeration consisting of 9-16 bees. In $\overline{pr}$, as well as in $\overline{A}$, these workers presented frenetic body shaking performing advance-retreat movements (more intensive in $\overline{pr}$ than in $\overline{A}$).

A fact related to worker body insertions into the cell was in $\overline{pr}$, when a worker was making body insertions in cells and spent more time in them, the queen tried to withdraw her, but, without any reactions from the worker, the first food discharge occurred. Instants before the first food discharge, the queen stayed at the lower part of the brood cell and touched its edge with her antennae.

The $\overline{pr}$ duration was 143.0 ± 183.5 sec., about 2.4 min (4 < value > 585 sec., n =25). In 26.5% of the cases, the duration of $\overline{A}$ was the same as that of $\overline{pr}$.

The number of worker body insertions into cells was 9.4 ± 9.3 (n=28) and the number of queen inspections was 1.2 ± 0.5 (n=28), while the duration of worker body insertions was 3.9 ± 2.7 (n=263) and that of queen inspection was 4.5 ± 2.2 (n=34). These observations confirm that, in the course of the oviposition process, there was an increase of agitation by workers.

Provisioning phase ($\overline{p}$). During food discharge, the queen touched workers with her antennae and, occasionally, with her forelegs. The queen did not display stroke or wing shaking. She inspected the cell after the first food discharge. Moreover, the queen who stayed at the cell edge took another position, staying 1/4 lower than the collared cell. In *M. c. manaosensis,* the queen could sometimes withdraw from the cell immediately after the first discharge or later (Sakagami & Oniki, 1963).

The worker's postdischarge withdrawal was performed slowly. The type of discharge in *M. c. fasciculata* was successive (P_C). The duration of phase $\overline{p}$ was 107.8 ± 34.0 (80 < value > 218 sec., n = 24). The number of discharges was 16.1 ± 1.4 (14 < value > 20 discharges, n = 24). As to the duration of each discharge, the value found was 1.5 ± 0.7 (1 < value > 4 sec., n = 104).

Postprovisioning phase ($\overline{ps}$). After the queen's brief inspection in the cell containing deposited food, a worker could lay an egg in the middle of the food. The color and position of this worker's egg was the same as that of the egg laid by the queen, while its size was smaller than the queen's egg. The same was observed by Camillo-Atique (1974) in *M. r. rufiventris*. The number of worker eggs in each cell was 1.2 ± 1.0 (0 < value > 5 eggs, n = 114). The number of worker eggs in each oviposition process was 6.6 ± 2.8 (1 < value > 12 eggs, n = 21). The duration of worker oviposition was 4.1 ± 1.2 (3 < value > 7 sec., n = 22).

In this phase, ingestion of larval food by the queen also occurred after a brief inspection in the fed cell. The time spent on such ingestion was 3.4 ± 2.2 (1 < value > 13 sec., n = 37). When worker oviposition finished, the queen ingested the egg; the time spent was 16.9 ± 14.7 sec. (3 < value > 107 sec., n = 61). The duration of $\overline{ps}$ was 28.1 ± 21.4 (3 < value > 80 sec., n = 24).

Oviposition phase ($\overline{o}$). After the ingestion of larval food, oophagy or a simple

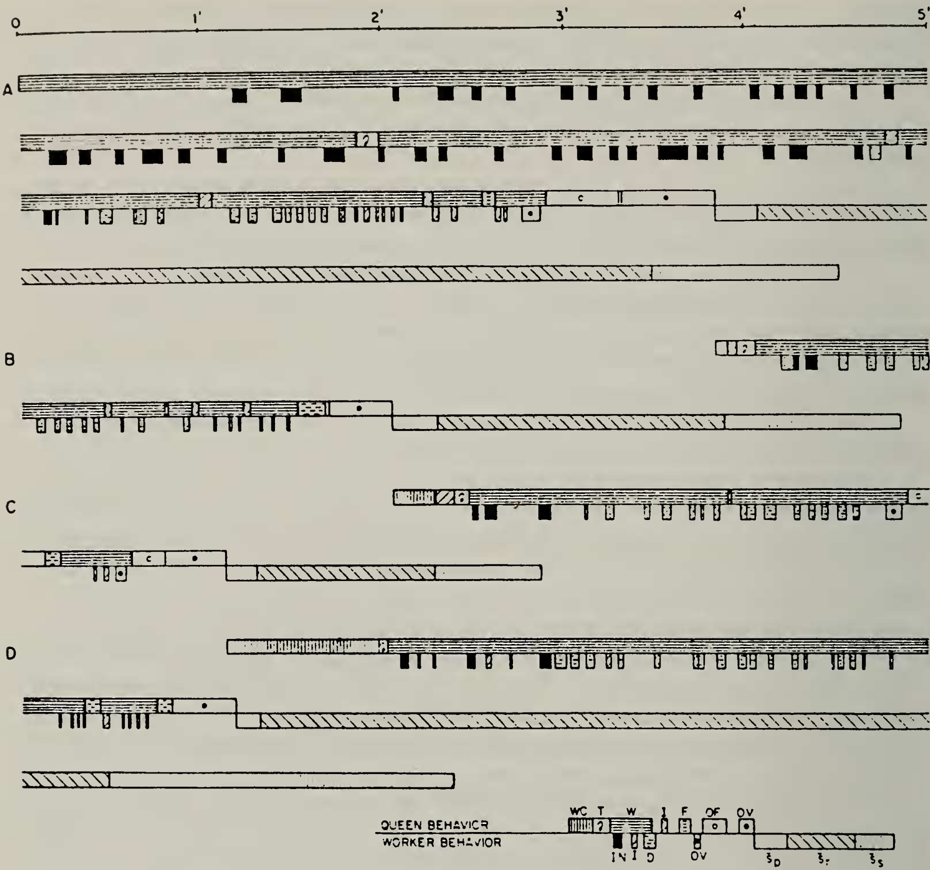

Fig. 3. Behavioral sequence in the POP with 4 cells (A,B,C,D) in *Melipona compressipes fasciculata* : D, food discharge; F, food ingestion; I, cell inspection; IN, body insertion into the cell; OF, oophagy; OV, oviposition; s_p, preoperculation subphase; s_r, rotation subphase; s_s sidework subphase; T, turning around cell; W, waiting at the edge of cell; WC, walking on brood comb. Such sequence starts in the pr phase.

inspection, the queen oviposited her egg in vertical position in the center of the cell, presenting wing shaking; the time spent on queen oviposition was 19.8 ± 4.6 (11 < value > 42 sec., n = 46).

Sealing phase ($\overline{s}$). As soon as the queen oviposition finished, a worker performed its operculation with her metasoma in the cell. There were three subphases in this behavior: $\overline{s_p}$, $\overline{s_r}$ and $\overline{s_s}$. The sealing time durations by workers were: total - $\overline{s}$ = 436.1 ± 164.5 (237 < value > 928 sec., n = 21); $\overline{s_p}$ = 18.6 ± 7.6 (5 < value > 39 sec., n = 21); $\overline{s_r}$ = 283.6 ± 62.8 (181 < value > 401 sec., n = 21); $\overline{s_s}$ = 133.9 ± 100.6 (51 < value > 488 sec., n = 21).

The provisioning and the temporal sequence in the oviposition process (fig.3) in *M. c. fasciculata* had a similar behavioral sequence to those of other *Melipona* species: cell construction, $(\overline{Q}+\overline{T}+\overline{P})$ period, arousal, preprovisioning, provisioning, postprovisioning, oviposition and sealing phase. There were also worker ovipositions.

Some ritualized queen/worker behaviors which were similar to those of other *Melipona* up to now studied were shown. This species presents successive cell construction and exclusively batched oviposition process (C_cB_e) - a singular pattern among all species of *Melipona*.

Acknowledgments. To S. Mateus for technical help. This work was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação de Amparo a Pesquisa do Estado de São Paulo (FAPESP).

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Recebido em 18.12.1996; aceito em 17.12.1997.